Additive influence of extreme events and local stressors on coral diversity in the Mesoamerican Reef during the last decade

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Abstract

Losing coral diversity is one of the most important consequences of coral reefs’ ongoing degradation. Alternate: As the planet enters its sixth global extinction event, the loss of biodiversity due to coral reef degradation becomes of paramount importance. However, the loss of coral species diversity and its relationship to multiple global and local stressors remains largely untested on different temporal or spatial scales. This study evaluates the change in coral species diversity and its relationship to different stressors and habitat characteristics, using ecological data from 73 sites in the Mesoamerican Reef (MAR) and a variety of potential explanatory variables derived from remote sensing. We found a loss of coral diversity in the period analyzed, from 2010 to 2018. In addition to a decrease in diversity, there was also a considerable change in coral assemblages. The coral reefs that presented a greater loss of species were those with higher initial diversity and those with a higher number of annual bleaching risk events. Surprisingly, coral reefs exposed to hurricanes and turbidity with intermediate magnitude did not experience the same loss in diversity; some reefs even experience an increased diversity in this timeframe. The rate of increase in macroalgal cover was related to the decrease in coral diversity. Our results highlight the need to protect reefs with high diversity and constantly exposed to high heat stress events. These reefs should be considered sites of relevance in future conservation plans in the current context of global environmental change.

Introduction

Coral reefs are among the most diverse (Fisher et al. 2015) and valuable ecosystems in the oceans (de Groot et al. 2012). Different stressors have caused constant degradation in these ecosystems, resulting in a loss of coral cover, structural complexity, diversity, and functionality (Bellwood et al. 2004; Hughes et al. 2017; Brandl et al. 2019). Currently, coral reefs are facing an era in which human actions dominate, characterized by global environmental change in which there are multiple drivers of ecosystem change (Hughes et al. 2017). With this high rate of change and degradation, assessing and predicting vulnerability to diversity loss is critical to recognize the negative impact on biodiversity, the function, and ecosystem services provided by coral reefs (Carpenter et al. 2008; Cardinale et al. 2012; Brandl et al. 2019), which include food security, livelihoods, and coastal protections for hundreds of millions of people globally.

With coral reefs, the main taxonomic group responsible for the construction of these ecosystems, the scleractinian corals, is a group particularly vulnerable to extinction (Carpenter et al. 2008; Huang 2012; Foden et al. 2013; Raja et al. 2021). This group has been highly impacted in recent years (Carpenter et al. 2008; Huang 2012; Hughes et al. 2017). Losing coral species would put at risk the entire ecosystem and multiple services that coral reefs provide to humans (Hughes et al. 2017; Brandl et al. 2019). The loss of coral diversity can cause harmful effects on coral reefs, such as a phase shift from coral to algae, reduction of resilience, and loss of ecological functions (Bellwood et al. 2004; Brandl et al. 2019; Sheppard et al. 2020). The current situation of high ecosystem degradation and multiple stressors
demands adequate knowledge of the drivers of change in the diversity of this fundamental biological group for coral reefs.

Several studies have advanced the determination of extinction risk and loss of diversity of corals based on modelling intrinsic vulnerability considering functional characteristics, sensitivity to stressors, and phylogenetic relationships (Huang 2012; Foden et al. 2013; Raja et al. 2021), as well as the vulnerability according to the decline of their populations, the degree of their rarity, and the reduction or size of their geographic distribution (Carpenter et al. 2008; Dietzel et al. 2021). However, few studies have directly analyzed the effect of exposure to different stressors on changes in the diversity of reef-building coral species. Some of these studies highlight the importance of some stressors, such as heat stress and ocean acidification, which can cause a considerable decrease in coral diversity (Vega-Rodriguez et al. 2015; Sunday et al. 2017; Sheppard et al. 2020). In addition, different local stressors have been identified as potential drivers of coral diversity loss, noting that human population density, excessive nutrient inputs, and coastal development can reduce coral diversity (Tomascik and Sander 1987; Edinger et al. 1998; Déath and Fabricius 2010; Darling et al. 2013). Other environmental factors such as depth, hydrodynamics, and exposure to hurricanes and storms can also be associated with changes in coral diversity patterns and a loss of coral diversity (Huston 1985; Rogers 1993; McField 2001). They may have an adverse effect if there is high exposure, but may even increase diversity if the disturbances are intermediate (Huston 1985; Rogers 1993). In addition, several outbreaks of coral diseases have caused local extinction, resulting in a loss of diversity (Aronson and Precht 2001; Estrada-Saldívar et al. 2020; Heres et al. 2021).

The precise description of diversity and the identification of its major drivers is fundamental for the management and conservation of coral reefs (Nyström et al. 2008; Nyström and Darling 2010; McClanahan et al. 2012). In this sense, the main objectives of the present work are: 1) the description of the change in the diversity of scleractinian corals and 2) the identification of the main drivers of change in the diversity of corals. For this purpose, we used numerical methods to describe the change in coral diversity and species composition and a multi-model assessment approach to identify the main drivers and characteristics linked with the change in coral diversity. Different potential drivers of change in biological diversity were considered, such as exposure to heat stress, exposure to storms and hurricanes, indicators of water turbidity, indicators of ecological condition (change in macroalgae and initial diversity), depth, as well as other potential local stressors associated with human population density and potentially moderated by management regimes within Marine Protected Areas (MPAs).

**Methods**

**Dataset of coral species**

Ecological data collection followed the AGRRA V5 protocol, which includes six, ten meter linear point intercept transects per site, with 100 data points per transect, according to the (Lang et al. 2010). This information is part of the long-term monitoring led by the Healthy Reefs Initiative.
(https://www.healthyreefs.org/cms/), which contains information from hundreds of reefs in the MAR, although not all are repeated during each assessment period. Data filtering and quality control process comprised eliminating all transects or sites with incomplete information (3 sites without dates and code) and those transects with over 50% sediment/sand cover (34 transects), as these transects do not characterize reef areas and are recommended to be avoided in the AGRRA method (Lang et al. 2010). Finally, only sites with ≥ 3 transect units were considered. Within this database, the sites re-sampled at least four times in different periods were selected for the analysis, getting 73 reefs used for the temporal comparison and analysis of the change in coral diversity (Fig. 1).

**Temporal comparison of coral diversity**

Three diversity indices were calculated for each of the reefs in each of the time periods considered: 1) species richness = mean number (mean value is generated from the values recorded in each transect) of different coral species surveyed in each reef; 2) Hill’s diversity number 1 (N1) = diversity measure which considers each species exact proportional abundance (equivalent to Shannon diversity index); and 3) Hill’s diversity number 2 (N2) = diversity considering each species, with an exaggerated weighted based on its abundance (equivalent to the inverse Simpson index) (Hill, 1973; Jost, 2006; 2007). We performed hypothesis testing to determine the difference in diversity between periods. First, Shapiro Wills and Levene’s tests were performed to test normality and homogeneity of variance (Royston 1995). Because the data did not meet the assumptions evaluated, robust nonparametric tests were chosen. In this sense, a heteroscedasticity one-way repeated measures ANOVA was applied for trimming means. This test allows a robust comparison of dependent samples that do not have homogeneity of variance, besides applying a post-hoc test (Mair and Wilcox 2017). All the analyses were performed with functions present in the “vegan” (Oksanen et al. 2016) and “WRS2” (Mair and Wilcox 2017) packages of the R statistical program (R Core Team 2017).

As an additional analysis to identify the change in coral diversity and composition, temporal beta diversity was calculated by analyzing the total temporal variance in coral species composition and its components following Legendre (2014). For this analysis, we used the beta.div.comp function of the “adespatial” package of the R statistical program, which allows us to identify the components of beta diversity. The index used for this analysis was the Ruzicka index (D_R) of the Podani family of beta diversity indicators, useful for quantitative data (abundance or proxies of biomass) (Legendre 2014). From this indicator, we obtained the coefficients of similarity, replacement, and differentiation for each reef, comparing the composition of coral species between the first (2010 to 2012) and the last period (2018).

**Potential drivers of coral diversity change**

Different metrics representing global and local stressors related to both extreme events and chronic pressures were considered to identify the causes of the change in diversity. For this purpose, remote sensing data and socio-ecological datasets available from organizations were considered (Table 1).
Table 1
Drivers and characteristics of the reef considered.

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<tr>
<th>Components</th>
<th>Variables</th>
<th>Database</th>
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<tbody>
<tr>
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<td>Number of storms and hurricanes between sample dates</td>
<td>International Best Track Archive for Climate Stewardship (IBTrACS; <a href="https://www.ncdc.noaa.gov/ibtracs/">https://www.ncdc.noaa.gov/ibtracs/</a>).</td>
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<td>Maximum wind in storms between sample dates</td>
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<td></td>
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<td>Max wind in storms from 1985 to 2010</td>
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<td>Waves</td>
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<td>Significant wave height information from the ERA5 reanalysis data (<a href="https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?tab=overviewundefined">https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?tab=overviewundefined</a>).</td>
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**Hurricanes and storms**

The International Best Track Archive for Climate Stewardship (IBTrACS; https://www.ncdc.noaa.gov/ibtracs/) database was used, which consists of vector type information for each of the storms and hurricanes. First, only hurricanes with a distance less than or equal to 30 km from
the reef were selected; recognized as the area of major influence of hurricanes on the reefs (Gardner et al. 2005; Edwards et al. 2011; Kjerfve et al. 2021). Different metrics representing exposure were generated considering the information of hurricanes in a buffer of 30 km. The number of hurricanes and storms that occurred in the period between the dates sampled was obtained. The number of hurricanes that occurred from 1985 to the first sampling date, the maximum value of winds that occurred between the dates sampled and the maximum wind intensity identified during the period from 1985 to the first sampling date were also identified. Finally, the time since the last hurricane or storm occurred was calculated, as well as the average return time between hurricanes (Table 1).

**Wave height**

As a measure of wave dynamics and its potential effect on corals, we considered significant wave height information from the ERA5 reanalysis data obtained from the Copernicus website (https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?tab=overview&undefined). This information comes in raster format with hourly data layers at a spatial resolution of 0.50°. The reanalysis data from this database is generated from a model that evaluates and predicts different wave components in both oceanic and coastal waters. The model presents as output different wave parameters, among which is the significant wave height (in meters) combining all wind waves and swells. This parameter represents the average height of the highest third of the surface waves, a useful metric for determining the sea state. We used the maximum monthly composite values of the significant wave height (in meters) combining all wind waves and swells as final indicators.

**Proxy of water clarity**

As an indicator of turbidity or clarity of the water, we used the diffuse attenuation coefficient (Kd$_{490}$) in m$^{-1}$, MODIS-Aqua raster information with a spatial resolution of 0.04° and weekly composites (https://modis.gsfc.nasa.gov/data/dataprod/kd_490.php). Based on the weekly composite values, monthly averages were generated. A buffer of 5 kilometers was applied to consider all pixels within this distance to extract and calculate the necessary metrics. This procedure allows a better representation of turbidity values near the reefs (Geiger et al. 2021). A threshold value of 0.30 m$^{-1}$ was taken to identify the "turbid" months. This threshold is a high value that is not usually present in many of the reefs in the MAR or the Caribbean (Rivera-Sosa et al. 2018; Geiger et al. 2021), in addition to being a value close to the limit for very turbid areas (0.50 m$^{-1}$) in the Caribbean (Chollett et al. 2012).

**Heat stress exposure**

For generating different heat stress metrics, the CoralTemp Sea Surface Temperature dataset of the Coral Reef Watch program with daily raster information and a resolution of 0.05° (https://coralreefwatch.noaa.gov/index.php) was used. A buffer of 5 kilometers was applied to extract and calculate the necessary metrics. This approach considers all pixels within this distance to calculate the metrics. The indicator used was Degree Heating Weeks (DHW), which quantifies the accumulated thermal stress by adding the positive thermal anomalies above 1°C of the climatological value of the
hottest monthly mean (e.g., mean of SST in September = 29.02), for 84 days (12 weeks) and divided by 7 to express the values per week. The metrics calculated were the maximum Degree Heating Weeks (DHW), the number of annual bleaching risk events (> 4°C-weeks), the number of annual mortality risk events (> 8°C-weeks), and the years since the maximum DHW occurred were calculated for the period between sampling dates (2010–2012 and 2018) and the period before the sampling (before 2010–2012). These metrics are important indicators of heat stress and are often good predictors of coral reef condition (Eakin et al. 2010; Muñiz-Castillo et al. 2019).

**Human density**

As a potential proxy for local stress due to population and development of human settlements, the annual human population density data with a resolution of 100 meters was used (https://www.worldpop.org/project/categories?id=3). To extract and calculate the necessary metrics, a buffer of 50 kilometers was applied, to consider all pixels within this distance to calculate the metrics (Bruno and Valdivia 2016). The following were calculated as indicators: 1) the change in human population from 2010 to 2018, 2) the 2010 human population, and 3) the change in human population from 2000 to 2010 as indicators.

**MPA information**

The MPAtlas data was used as a source of information on the conservation status or protection of the reefs. This database is a GIS with vectorial data of MPA information (https://mpatlas.org/). It combines self-reported data submitted by countries to the official World Database on Protected Areas (WDPA). In this case, the information obtained directly from the vector layer of the MPAtlas was used; in the case of two overlapping MPAs, priority was given to using the information from the oldest MPA.

**Habitat and ecological metrics**

Different variables representing potential drivers of diversity change were also obtained from the monitoring data collected by the Healthy Reefs Initiative using the AGRRA protocol. Among the metrics considered are changes in macroalgal cover as a potential indicator of nutrient excess (although this is confounded with level of herbivory), initial diversity, and depth. With macroalgal cover, it is necessary to emphasize that this variable can be a response to distinct aspects related to the dynamics and processes of coral reefs. On the one hand, it is a response to bottom-up processes because of the increase of nutrients reflecting the potential increase of nutrients (Suchley et al. 2016; Martínez-Rendis et al. 2016; Arias-González et al. 2017). However, it is also a response to a lack of top-down control because of the loss of herbivores in the ecosystem which causes the increase of macroalgae (Bellwood et al. 2004; Hughes et al. 2017). Depth is a habitat characteristic that can be linked and act synergistically with different stressors, such as heat stress or hurricanes (Riegl and Piller 2003; Bongaerts et al. 2010).

**Relationship between drivers and change in coral diversity**

All the metrics mentioned above were considered as predictor variables, and linear regression models were performed to recognize which variables contribute the most to the change in coral diversity,
considering the N1 of Hill’s diversity as the response variable. The N1 of coral diversity was considered because it considers a weighting according to the abundance of coral species (Jost, 2006; 2007). In the case of the response variable represented by the N1 of coral diversity, the Shapiro-Wilks test was performed to verify that the distribution was Gaussian or “normal” (Royston 1995). In addition, different visual evaluations such as scatterplots and histograms were performed. Linear models were chosen as the best option because they offer the most interpretable information, adding that we preferred these models to generalized additive models (GAM) because we were looking for greater simplicity in the number of variables and constants used in the model.

The relationship between the predictor variables was analyzed, for which scatter plots were made, and correlation analysis (Supplementary Fig. 1) combined with Principal Components Analysis (PCA; Supplementary Fig. 2) made it possible to recognize a priori which variables were collinear. It was established that the variables that presented more than 0.60 in the correlation coefficient would not be used in the same model (Zuur et al., 2010; Dormann et al., 2013). All combinations of linear regression models (~730,000 models) were performed, establishing additive models among all the non-collinear variables. In addition, different interactions that could have a potential effect on diversity change were also evaluated, such as interactions between heat stress with depth or wave height, in total over 30 interactions within linear models were considered. All the models obtained were compared from a multi-model approach. Different indicators of the models, such as the coefficient of determination (R²), the corrected Akaike Information Criterion (AICc), the ΔAICc, and the Weight of all the models were obtained (Burnham and Anderson 2002; Barton and Barton 2013). For this analysis the “MuMIn” package was used (Barton and Barton 2013), and functions present in basic packages of the R statistical program (R Core Team, 2017).

The best models obtained were analyzed to check the statistical significance of the terms obtained, the distribution of the residuals, and the spatial autocorrelation. All the terms were significant in the “best models”, besides presenting an acceptable distribution of residuals and no evidence of spatial autocorrelation in the residuals obtained. The presence of spatial autocorrelation was assessed from a spline correlogram using the functions of the “ncf” package (Bjornstad and Cai, 2020) of the R statistical program (R Core Team, 2017).

Results

Fifty coral species were recorded from the total observations (Supplementary Table 1). The temporal variation analysis showed a decrease in species richness and diversity over time (with a decrease of about one species in the diversity indicators between the period 2010 to 2018). The difference in richness and diversity was significant between the diversity observed in the first period (2010–2012) and all the other periods analyzed – which were not significantly different from each other (Fig. 2a; Supplementary Tables 2 to 5). From 2010 to 2018, the mean change of coral diversity based in N1 of hill numbers was −0.52 (SD ± 32%) and the mean proportion of diversity change was −9.34% (SD ± 32%) of species per site. The species that have dominated the coverage and were the most frequent are *Porites astreoides*,
Siderastrea siderea, Agaricia teunifolia, Agaricia agaricites, Porites porites, and species of the genus Orbicella (Supplementary Table 1).

The results of the temporal beta diversity (change in species composition from 2010 to 2018) analysis showed that over 50% of the reefs present a low temporal similarity (< 30%), which expresses a considerable change in species composition between the first and the last period analyzed (Fig. 2b and c). This change in species composition was dominated by a replacement in abundance among species in most reefs (Fig. 2b and c). However, the component of total abundance differentiation was also relevant in different reefs (Fig. 2b and c). Most species show a decrease in the frequency of occurrence along the reefs, having 33 species with a decrease in frequency (Supplementary Fig. 3). Some species stand out in the decrease of their presence as of Agaricia humilis, Agaricia agaricites, Porites divaricata, Millepora complanata, Colpophyllia natans, Pseudodiploria clivosa, Millepora alcicornis, and Porites furcata.

Practically none of the species were considerably more frequent, as all occurred on three other reefs at maximum during 2018 versus 2010. With the relative cover change between 2010 and 2018, we observed that the biggest losers were Orbicella faveolata, Millepora complanata, and Agaricia agaricites, while the biggest gainer was Siderastrea siderea. However, no considerable change in relative species cover was observed. This underlines that although the pattern of dominance of coral species of the MAR remains similar, most species presented a considerable decrease in their presence on the reefs.

**Extreme events and local stressors in the MAR**

The period analyzed (from 2010 to 2018) was characterized as a period of high exposure to heat stress. Most reefs were exposed to at least one bleaching risk event during this period, and over 30% of the sampled reefs were exposed to two or more events (Fig. 3). Besides, reefs also showed moderate exposure to hurricanes and storms, with almost 60% of reefs exposed to at least one tropical storm. However, most of the hurricanes that passed near the reefs in the region were of low category. Only 12 of the reefs considered were exposed to hurricanes category one (> 64 knots), while 36 of the reefs considered were exposed to tropical storms (34 to 63 knots). These results coincide with the significant wave height measured in the ERA5 model output, thus observing a high sea state without extreme winds (Fig. 3). Based on the proxy of turbidity, we observed that most of the reefs considered presented clear waters, with maximum monthly mean values of Kd-490 between 0 and 0.25, and only 7 reefs with values higher than 0.5 - considered as reefs with increased turbidity (Fig. 3). From 2010 to 2018, the increase of human population density close to the reefs (within a buffer of 50 km) presented high variation (Fig. 3), most of the reefs considered were close to human settlements with an increase of close to 50,000 habitants (~ 1,000 persons per 50 km²) over the entire MAR. There was high variability with most reefs experiencing fairly little change (both increases and decreases) in fleshy macroalgal cover.

**Drivers of coral diversity change**

From the multi-model selection analysis, six suitable models were identified to explain the change in coral diversity. These six linear regression models have an R² of between 0.60 to 0.63 and all have non-
collinear variables with coefficients significantly different from 0 (Fig. 4). Within these six models, the main variables identified as potential drivers of change in diversity were initial diversity, the frequency of annual bleaching risk, water turbidity, wind during storms and hurricanes, wave height, and size of MPAs. These variables were present in most of the final models. Besides these variables, change in macroalgae cover, historical (from 1985 to 2010) frequency of storms, and historical (from 1985 to 2010) annual bleaching risk events were also identified as relevant metrics. We observed that the most important characteristic was initial diversity and exposure to annual bleaching risk events, with the most diverse and exposed reefs being those with the greatest loss of coral species. The size of the MPAs was found to be negatively related to the change in diversity, observing that reefs present in larger MPAs have a greater loss of coral species. In addition, it was identified in Model 4 that the reefs in which macroalgae coverage increased showed a decrease in coral diversity. Positive relationships were observed between wind intensity during storms, wave height, and the proxy of turbidity.

Discussion

The coral diversity recorded in this work represents most of the species present throughout the Caribbean. About 50 scleractinian coral species are identified in research realized in the wider Caribbean (Huang and Roy 2015; McWilliam et al. 2018). We found a substantial loss of coral diversity in the period analyzed. Both species richness and diversity considering abundance (Hill’s N1 and N2 of diversity) decreased in the MAR coral reefs. Additionally, we note that most of the species show a considerable reduction in the frequency of occurrence along the MAR, which could express a simplification of the coral composition in the region, leaving a lower diversity in most of the coral reefs. It is important to note that in this work we used an intercept point method, which may have a lower detection of coral species than other methods that consider a larger area, such as belt-transects. However, the accumulation curve of the analyzed periods shows that the diversity seems to be well represented at the MAR scale (Supplementary Fig. 4), but it is possible that the most cryptic species have not been correctly represented. We recommend that future work consider other monitoring methods that present a better identification, especially of the rarest species, to better capture the loss of diversity in these ecosystems. Losing diversity of reef-building corals has been observed in different regions of the world, such as reefs in the Indo-Pacific and Florida (Vega-Rodriguez et al. 2015; Sheppard et al. 2020). These losses have even led to local or regional extinction of several coral species (Glynn and De Weerdt 1991; Cramer et al. 2020), which can also reduce reef ecosystem functionality and processes (Bellwood et al. 2004; Brandl et al. 2019; Sheppard et al. 2020). Our results underline the importance of considering coral diversity as a potential indicator of the current degradation of coral reefs. Most reef assessments focus on aggregated coral cover as the main indicator of coral reef condition (Gardner et al. 2003; Wilkinson 2008; Souter et al. 2020). Still, the potential loss of diversity in the medium term and the repercussions this may have on the ecosystem are being overlooked.

The major drivers of the change in coral diversity were initial diversity and the number of annual bleaching risk events, which were related to a greater loss of diversity during the period analyzed. First, the most diverse coral reefs were those most likely to lose diversity. Different authors have suggested that
diversity is a good indicator of resilience to disturbances with coral reefs, based on the premise that greater diversity tends to offer a wider variety of functional responses (Nyström et al. 2008; Roff and Mumby 2012; McClanahan et al. 2012; Mora et al. 2016). Initial diversity is fundamental in the trajectory of temporal change in diversity that a community may have because of exposure to different disturbances; different levels of initial diversity may even interact with different degrees of disturbance and cause different trajectories of change (Randall Hughes et al. 2007). It has been hypothesized that communities with a low recruitment rate, high exposure to disturbance, and high initial diversity are communities with a very high decline in diversity because of ecological disturbance events (Randall Hughes et al. 2007). Our results highlight the importance of protecting the most diverse reefs, as they may be potentially vulnerable to future disturbances, because in the case of the MAR, high coral diversity is not synonymous with resistance capacity.

Heat stress, as represented by the number of annual bleaching risk events (years with DHW > 4°C - weeks) was an important driver of coral diversity loss. Exposure to heat stress affects corals in diverse ways. First, this stressor causes bleaching events and often mass mortality in different reefs worldwide (Baker et al. 2008; Eakin et al. 2019). Heat stress causes the loss of coral cover when exposure is very high, for example, in the Caribbean when reefs are exposed to events of a magnitude greater than 8°C – weeks (Eakin et al. 2010). Besides, exposure to extreme heat has also been associated with loss of diversity in different reefs worldwide (Glynn and De Weerdt 1991; Vega-Rodriguez et al. 2015; Sheppard et al. 2020). It is worth mentioning that the MAR was exposed to high heat stress during the period analyzed. In fact, from 2015 to 2017 the reefs of this region were exposed to unprecedented heat stress events, emphasizing that much of the Mesoamerican reef system experienced its maximum exposure during this period (Muñiz-Castillo et al. 2019). The context of exposure to extreme oceanic heat events during the analyzed period initiated to be determinant in the change of coral diversity because the high frequency of these heat stress events may be one of the main drivers of degradation in the reefs of the MAR. This result highlights the importance of establishing management and conservation measures that consider mitigation strategies for the effects of climate change on coral diversity in the region.

On the other hand, wind recorded during hurricane events was positively associated with the change in diversity. Distinct reasons can explain this. The first is that the corals were not considerably exposed to hurricanes and storms during the analyzed period (2010 to 2018). Most coral reefs sampled presented between 0 to 3 hurricanes within a radius of 30 km. Only ten of the reefs monitored had a maximum wind speed during storms of over 60 knots, with most of the reefs exposed to intermediate levels of wind exposure during storms and hurricanes, recognized as non-severe degrees of exposure for the condition of coral reefs (Gardner et al. 2005). These reefs suffered from intermediate magnitude disturbances to hurricanes, and therefore no loss of diversity occurred. Connell's classic intermediate disturbance theory (Connell 1978) and field research on coral reefs indicate that intermittent and intermediate magnitude exposure to hurricanes allows maintaining a greater diversity of corals (Huston 1985; Rogers 1993).

Recent analyses highlight the null negative effect of hurricanes and storms on Caribbean coral reefs during the last decade. This null impact is mainly because many of these reefs present a high state of
degradation and only the most resistant corals to this type of extreme event are present in the region's reefs (Mudge and Bruno 2021). However, it is recognized that high magnitude (strong winds) of exposure to hurricanes can be an important driver in the degradation of Caribbean coral reefs (Mumby 1999; Gardner et al. 2005; Edmunds 2019; Reguero et al. 2019). Besides being an extreme event of great relevance in the socio-economic vulnerability of the region (Reguero et al. 2019). With MAR reefs, it is recognized that the effect of hurricanes may not be as severe as that of heat stress, although the combined effect of these two could have a considerable negative effect on these ecosystems (Edwards et al. 2011) as recorded in Belize due to the 1998 bleaching event and hurricane Mitch (McField 2001). Cumulative exposure to hurricanes and storms can cause different effects, ranging from direct removal and death of corals from direct wave action (Gardner et al. 2005; Madin and Connolly 2006; Edmunds 2019) to decreasing coral recruitment (Mumby 1999). Hurricanes can have a negative effect on corals that can be seen even in long-term periods, causing a decrease in coral cover even several years after the impact occurs (Gardner et al. 2005). These contrasting results suggest that if exposure to hurricanes is intermediate the effect on diversity may be positive (increase during the period considered). Yet, if exposure is remarkably high over a historical period this may affect reefs even in the long-term causing a decrease in coral diversity.

Other indicators linked to potential local impact because of sediments or nutrients were also highlighted as relevant drivers of change in diversity. With these indicators, contrasting results were observed. The water turbidity proxy (Kd-490) showed a positive relationship with coral diversity, with the more turbid reefs experiencing an increase in coral diversity. This result may seem contradictory, but the explanation for this pattern is that few reefs in the MAR have remarkably high turbidity. During the entire period analyzed, less than 25% of the reefs showed a value higher than 0.30 m$^{-1}$, which expresses relatively low exposure to turbidity in the reefs of the region (Chollett et al., 2012b; Rivera-Sosa et al., 2018; Geiger et al., 2021). Although water turbidity can be an important stressor on corals (Fabricius 2005), there is also some research indicating that “turbid water reefs” have been more protected from solar radiation and small scale heat stress (Sully and van Woesik 2020). We suggest it is also possible that these “toughened” reefs, normally exposed to fluvial runoff may have been conditioned to this stress, and that the more turbid surface layer runoff can act to insulate these corals from heat and solar radiative stress because the surface layer infrequently interacts with the seafloor. Several of the more turbid reefs (located in the coastal zone of Guatemala and Honduras) have some of the highest coral cover values in the MAR. (Mcfield et al. 2018; Rivera-Sosa et al. 2018). Therefore, this indicator does not correctly reflect the potential nutrient input because of human activities on the mainland. Considering metrics that represent nutrient, agrochemicals, or sediment proxies on reefs remains a critical area of opportunity in the MAR region. To date, very few regional-scale efforts have been able to model or represent the influence that land-based activities may have on the waters surrounding coral reefs, most notably the report by the World Resources Institute (Burke and Sugg 2006). Future efforts should focus on estimating or modeling the spatial distribution and the temporal variation of nutrients and chemical substances associated with human pollution, as this would be a great step forward in understanding the potential direct impact of human activities in the watershed or in coastal areas near coral reefs.
In this work, an indirect indicator of nutrient input was the change in macroalgal cover, observing a negative relationship with the shift in diversity (increase in macroalgae = decrease in diversity). It is recognized that with the MAR, the phase shift occurred in the coral reefs, in which the macroalgal cover is gaining ground over corals, is related to the constant input of nutrients because of coastal gentrification and human activities in the basin (Suchley et al. 2016; Martínez-Rendis et al. 2016; Arias-González et al. 2017). However, the change in macroalgal cover is also highly related to herbivory control, because if there is a loss of key herbivores it is possible that there is less top-down control (Bellwood et al. 2004; McManus and Polsenberg 2004; Brandl et al. 2019; Bruno et al. 2019), so we cannot be sure that the increase in macroalgae is only a cause of increased nutrient input.

In the results obtained in this work, the human population density and the change in the human population density were not selected as relevant drivers. Work on a global scale has shown that human population density near reefs is not directly related to the condition of coral reefs (Bruno and Valdivia 2016). In macroecological studies, indicators of human population density and human activities for potential local impact do not currently take nutrient inputs into account. The existing indicators are often only available at very large spatial scales, providing data at the country or regional level (Halpern et al. 2019; Cramer et al. 2020). This lack of consistent and frequent spatiotemporal data makes it difficult to analyze the relationship between local human activities and change in coral reef conditions or diversity, leaving a gap about the effect of direct impact because of nutrient inputs. Future research needs to develop more sensitive metrics that better represent nutrient inputs associated with human presence activities (Pawlik et al. 2016; Delevaux et al. 2018; Wolff et al. 2018; Bruno et al. 2019).

The results obtained showed a negative relationship between the size of the MPAs and the change in coral diversity. This negative relationship reflects that MPAs size is not an indicator of the corals' level of protection or conservation. Sometimes the size does not matter, as in the case of MPAs, the level of compliance and the time since the area was designated seem to be more critical (Bonaldo et al. 2017; Cortés-Useche et al. 2019). However, in some cases the size of the MPAs does not have a considerable effect or it is even possible to observe a positive effect in large MPAs (Halpern 2003). It is important to mention that, with this analysis, all management or conservation units were considered, including Ramsar areas and other designations. With the MAR, information is currently being generated and available with a better designation of the degree of protection by the Healthy Reefs Initiative, which could be incorporated into future work. This information would make it possible to evaluate the state of marine ecosystems in the region, as has been done in some regions, such as the Mexican Caribbean (Suchley and Alvarez-Filip 2018). Meanwhile, our results reflect that large MPAs appear to be ineffective in protecting coral diversity, especially because these large areas tend to have low operational capacity.

**Conclusion**

This study measured a 10% mean loss of diversity within the Mesoamerican Reef from 2010–2018. The main driver of loss in coral diversity was exposure to heat stress because, during the studied period, the region was exposed to unprecedented heat-stress events (Muñiz-Castillo et al. 2019). However, with the
indicators of exposure to local stressors, considerable technical limitations still inadequately represent these stressors, especially when working at macroecological scales. This consequence does not mean that there is no constant local pressure because in the region it is recognized that the impact because of human activities on the coast and nutrient inputs are among the main causes of phase shift in this ecosystem (Martínez-Rendis et al. 2016; Arias-González et al. 2017). The combined impact of these stressors could be more important (Hughes et al. 2017; Ortiz et al. 2018), so future work needs to consider the importance of local stressors, and it is necessary to look for proxies that better represent these stressors. These proxies need to be standardized and scalable to be used in studies conducted at regional scales.

We emphasize that in the case of the MAR, the reefs with the greatest diversity were those with the greatest loss of coral diversity, suggesting that more diverse reefs tend to be less resistant to different stressors. This highlights the importance of protecting the most diverse reefs and creating recovery strategies after the impact of different stressors. It is also necessary to generate more information in the region about the change in coral diversity at different spatial and temporal scales, as well as with the use of different methodologies to better identify patterns of change in the biodiversity of the region's reefs. It should be noted that this work only considers up to 2018. This time window limits the inclusion of what may be the current major stressor in the loss of coral diversity in the region, the Stony Coral Tissue Loss Disease (SCTLD). This disease has been affecting the Caribbean coral reefs (Alvarez-Filip et al., 2019; Estrada-Saldívar et al., 2021; Heres et al., 2021), so these results may need to be updated soon to incorporate the impact caused by SCTLD. Despite the limitations and the prospects to be fulfilled, this work provides a scientific basis of relevance for the conservation of marine diversity in the MAR region, and a multidimensional conceptual framework that allows the incorporation of multiple stressors causing a change in coral diversity. It highlights the importance of conserving highly diverse reefs, which can be affected when exposed to various global and local stressors, particularly when the intensity and frequency of these disturbances is growing.

**Declarations**

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**Authors’ contributions**

All authors contributed substantially to the conceptual design and implementation of the study. All analyses were conducted by A. Israel Muñiz-Castillo. The first draft of the manuscript was written by A. Israel Muñiz-Castillo. All authors edited and provided constructive input on subsequent versions of the manuscript. All authors have read and approved of the final manuscript.

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**Data Availability**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

**Conflict of interest**

The authors have no relevant financial or non-financial interests to disclose.

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Figures

Figure 1

Spatial distribution of the reef 73 sites surveyed.
Figure 2

Temporal variation of coral diversity. a) Alpha diversity temporal comparison. The first period includes observations made from 2010 - 2012, the second period includes observations made during 2013 - 2015, the third period includes observations made in 2016 and the last period includes observations made in 2018. The red asterisk represents the period significantly different from the others according to the robust ANOVA test (Supplementary Tables 2 to 5). Each of the points represents the value of diversity for each of the reefs. b) Triangular plots of the relative contribution (%) of abundance species replacement (Replacement) and changes in total abundance (Abundance) to the total temporal beta diversity using the Ruzicka index. Temporal beta diversity was calculated using the comparison of the coral assemblage between 2010-2012 and 2018. Each of the points on the triangle plot represents the percentage of the beta diversity component for each of the reefs, and the color palette represents the number of sites that share a similar value in beta diversity components. c) Boxplots of the distribution of temporal beta diversity (similarity) and the components (Abundance and Replacement).
Figure 3

Variation of values of stressors and drivers in the analyzed period from 2010 to 2018.

Figure 4
Multimodel evaluation and standardized coefficients of the uncorrelated predictors in the best linear models. a) Scatterplot of the values of the coefficient of determination and Delta AICc of the thousand best models. The dots in different colors represent the six models selected. b) Plot of the standardized coefficients of the variables identified in the six best models.

Supplementary Files

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